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Rice Growth, Yield and Photosynthetic Responses to Elevated Atmospheric Carbon Dioxide Concentration and Drought

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Rice Growth, Yield and Photosynthetic Responses to Elevated Atmospheric Carbon Dioxide Concentration and Drought

J. T. Baker
L. H. Allen, Jr.

SUMMARY. Rice is a major food crop that should respond favorably to expected future increases in atmospheric carbon dioxide concentration. Due to uncertainties in the timing and amounts of monsoonal rainfall, drought is common in some rainfed rice production systems. In this paper, we summarize results of experiments conducted by the University of Florida and USDA-ARS at Gainesville, FL, USA, where the effects

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and interactions of elevated atmospheric carbon dioxide concentration and periodic drought were examined in relation to grain yield and canopy-scale gas exchanges, specifically photosynthesis, respiration, and evapotranspiration.

Elevated CO₂ increased rice growth, grain yield and canopy photosynthesis while reducing evapotranspiration by about 10%. During drought stress cycles, this water savings under elevated CO₂ allowed photosynthesis to continue for one to two days longer compared with the ambient CO₂ treatment. Rice canopy photosynthesis saturated with respect to CO₂ near 500 $\mu\text{mol mol}^{-1}$ and we found little evidence of photosynthetic acclimation or down-regulation in response to long-term CO₂ enrichment treatments of 350 and 700 $\mu\text{mol mol}^{-1}$. Under a much broader range of long-term CO₂ treatments (160 to 900 $\mu\text{mol mol}^{-1}$), a significant degree of photosynthetic down regulation was detected. Day-time CO₂ enrichment resulted in higher canopy dark respiration compared with the ambient grown controls when compared at a common, near ambient nighttime CO₂. We also detected a rapid and reversible, direct inhibition of canopy dark respiration rate with rising chamber CO₂ at an air temperature of 28°C. [Article copies available for a fee from The Haworth Document Delivery Service: 1-800-HAWORTH. E-mail address: <docdelivery@haworthpress.com> Website: <http://www.HaworthPress.com>]

KEYWORDS. Climate change, photosynthesis, respiration, water use, acclimation

INTRODUCTION

Rice paddies in Asia play a significant role in the global budgets of greenhouse gasses such as carbon dioxide (CO₂) and methane (IPCC, 2001). The atmospheric concentration of CO₂ was about 358 $\mu\text{mol mol}^{-1}$ in 1995 and is increasing by about 1.6 $\mu\text{mol mol}^{-1}$ per year or nearly 0.5% per year (Keeling et al., 1995). Work by Jones et al. (1994, 1999) and Mann (1999) suggests that there has been a 0.3 to 0.6°C warming of the earth's surface since the late 19th century. Compared with pre-industrial levels, atmospheric concentrations of CO₂ have increased by 30% (Houghton et al., 1996). This has led to projections of future increases in global air temperatures as well as potential shifts in regional scale precipitation patterns and the possibility of reduced soil water availability in some regions of the world (Wilson and Mitchell, 1987; Hansen et al., 1988).

Rice is the World's most important grain crop in terms of direct human food consumption. Rice is generally classified into four broad categories depending

on soil and water habitat: irrigated or paddy grown rice, lowland rainfed rice, upland rice, and deep-water rice. Of the total of 140 to 145 million hectares of land area planted to rice annually, roughly half or about 53% is grown as irrigated, flooded paddy rice, one-fourth as rainfed lowland rice, 10-14% as upland rice and about 6% as deep-water rice (IRRI, 1975, 1982, 1984). About 75% of the world's rice harvest comes from irrigated rice where the fields are flooded for much of the growing season.

Drought caused by uncertain monsoonal rainfall frequently reduces rice plant populations and final yield (IRRI, 1975). Excluding irrigated rice, about half of the world's rice land area depends on rainfall and is often subjected to drought stress (O'Toole and Moya, 1978; IRRI, 1982). Since soil water availability currently limits crop growth more than all other environmental factors combined (Mauney et al., 1979; Boyer, 1982), it is important to quantify the effects and possible interactions of water management practices with CO₂ upon major food crops such as rice.

The occurrence (or non-occurrence) of 'photosynthetic acclimation,' or 'down-regulation of photosynthesis,' in response to CO₂ enrichment is a naturally occurring phenomenon that, due to a lack of understanding, limits our ability to predict plant and ecosystem responses to CO₂ enrichment. In some plant species, photosynthesis was initially stimulated by CO₂ enrichment but then subsequently declined with continued CO₂ enrichment (Sage, 1994; Drake et al., 1997). One hypothesis put forward to explain this decline in photosynthesis following CO₂ enrichment is an end-product feedback inhibition of photosynthesis resulting from an imbalance between 'source' and 'sinks' for photoassimilates (Stitt, 1991; Bryant et al., 1998). Long-term CO₂ enrichment for rice and some other species can result in decreases in the content of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) and other photosynthetic pigments as well as decreases in Rubisco activity (Besford et al., 1990; Rowland-Bamford et al., 1991; Bowes, 1993). There is much evidence that increases in tissue carbohydrate content under CO₂ enrichment modulates gene expression for many photosynthetic enzymes (Koch, 1996; Jang and Sheen, 1997; Moore et al., 1999).

Since 1987, numerous studies have been conducted at the University of Florida, USA on the effects of atmospheric carbon dioxide concentration on crop plants, including rice. For reviews of experiments aimed at determining the effects of CO₂ and air temperature on canopy-level gas exchange, growth and yield of rice, the reader is referred to Baker and Allen (1993a,b) and Allen et al. (1996). Our objective here is to summarize recent results of several papers that examined growth, yield and canopy gas exchanges (photosynthesis, respiration, and evapotranspiration) of rice canopies subjected to ambient and elevated CO₂ as well as periodic drought.

METHODS

Controlled Environment Chambers

Rice (cv. IR-72) plants were grown season-long in eight naturally sunlit Soil-Plant-Atmosphere-Research (SPAR) chambers at ambient ($350 \mu\text{mol mol}^{-1}$, 4 chambers) and elevated ($700 \mu\text{mol mol}^{-1}$, 4 chambers) CO_2 treatments. These chambers were constructed of an aluminum frame, canopy zone tops covered with transparent polyethylene terephthalate "Sixlight" film (Taiyo Kogyo Co., Tokyo¹). Above ground chamber dimensions were $2.0 \times 1.0 \text{ m}^2$ in cross section by 1.5 m in height. Each chamber top was attached to a lysimeter constructed of aluminum measuring $2.0 \times 1.0 \text{ m}^2$ in cross section and 0.6 m deep, to provide a water tight, flooded root environment for growing rice in paddy culture. Soil filled each lysimeter to a depth of 0.5 m and paddy flood water depth was maintained at 50 mm above the soil surface using a float-actuated water valve to supply deionized water to each soil lysimeter. The main chamber dimensions were $2.0 \times 1.0 \text{ m}^2$ in cross-section with a north-to-south sloping top that averaged 1.4 m in height, for a volume of 2.8 m^3 . The 0.05 m space above the flood water provided an additional 0.1 m of aerial volume and the air handling ductwork had a volume of 0.3 m^3 . In 1993, the full-wall doors of the south sides of each chamber were replaced with an access compartment that averaged 1.2 m in height with a $2.0 \times 0.5 \text{ m}^2$ base, which provided 1.2 m^3 of additional chamber volume. All together, the total aerial volume of each chamber was 4.4 m^3 . The calculated air exchange rate was 2.7 chamber volumes per minute.

Air was circulated from top to bottom within each chamber using fans located in external ducting. Exit duct air velocity was 3 m s^{-1} . Chamber dry bulb air temperature was measured with an aspirated, shielded thermocouple suspended 0.3 m above the canopy. Dew point air temperature was measured in the exit duct air stream with a dew point hygrometer (Dew-10, General Eastman Instruments). The air handling system, located in the external ducting contained cold- and hot-water heat exchangers and an electrical resistive-heat coil to control dew point and dry bulb air temperatures. Dew point was controlled to $18/12^\circ\text{C}$ (day/night) using the cold-water heat exchanger to remove excess humidity. Dry bulb air temperature was controlled to $28/21^\circ\text{C}$ (day/night) by reheating the air, as needed, using the hot-water heat exchanger and an electrical resistive-heat coil.

Rice paddies are a very weak net source of CO_2 to the atmosphere rather than a sink for CO_2 from the atmosphere. The biophysical reasons for this effect are described in detail by Baker et al. (2000a).

1. Use of trade or manufacturer's name does not imply endorsement.

Canopy Photosynthesis, Respiration and Evapotranspiration

The chamber system measured CO_2 using a common gas sampling system with infrared gas analyzers (IRGAs) for measuring CO_2 (Siemens, Ultramat 22P). Daytime chamber CO_2 was maintained by supplying pure CO_2 from a compressed CO_2 gas cylinder to mass flow controllers located in the external ducting of each chamber. The CO_2 injection rate was monitored by the mass flow controller which also functioned as a mass flow meter. Daytime canopy carbon exchange or net photosynthesis (P_n) was calculated from mass balance equations averaged every 300 s. Canopy gross photosynthesis (P_g) was calculated by adding daily estimates of canopy dark respiration (R_d) to P_n .

Each day near dusk, the controlled-environment chamber system was automatically switched from measuring photosynthesis to measuring canopy apparent dark respiration rate (R_d) during the night period from 1900 to 0600 h. During this night period, computer-control of chamber CO_2 by injections of pure CO_2 was suspended. Computer-controlled solenoid valves connected to high-pressure air-lines were used to control the opening and closing of air vent gates located in the ductwork of each chamber. At the end of each hour, during the night period, the air vent gates were opened and the chamber atmosphere was purged with ambient air driven by an electrical fan. The R_d was measured by automatically venting and resealing the chambers once an hour at night and monitoring the rise in chamber CO_2 from canopy respiration. The condensate from the cooling coils used to control dew point air temperature (DPT) passed through tipping bucket rain gauges to calculate evapotranspiration rate (ET). All canopy gas exchange measurements were expressed on a ground area basis. Specific methods for controlling chamber environmental set points (hardware, control algorithms) as well as the quality of those environmental controls are given by Pickering et al. (1994).

Tests for Photosynthetic Acclimation to CO_2 Treatment

To test for possible photosynthetic acclimation, a short-term CO_2 cross-switching experiment was conducted from 29 Aug. to 2 Sept. 1994 (45-49 days after planting, DAP), prior to the drought stress treatments (Baker et al., 1997b). Each morning from 0600 to 1200 EST, the CO_2 in each chamber was controlled to 160, 1000, 250, 700, and 350 $\mu\text{mol mol}^{-1}$ on 45 through 49 DAP, respectively. In this way, P_g light response of the long-term 350 and 700 $\mu\text{mol mol}^{-1}$ treatments could be compared at a range of common short-term CO_2 . After 1200 h, the CO_2 control set-point was returned to its original long-term growth concentration treatment. Canopy P_g light response curves were fit with second order polynomials using the NOINT option of the GLM procedure pro-

vided by the SAS Institute (Cary, NC). These results are also compared to results from a previous experiment conducted in 1987 on the rice cultivar IR-30.

In 1987, the rice cultivar IR-30 was grown season-long in subambient (160 and 250) ambient (330) and superambient (500, 660 and 900 $\mu\text{mol mol}^{-1}$) CO_2 treatments. Tests for photosynthetic acclimation were conducted from 62 to 67 days after planting when canopy net photosynthesis (P_n) was compared by short-term cross-switching of CO_2 treatments to 160, 300, and 660 $\mu\text{mol mol}^{-1}$. Details of this experiment are given by Baker et al. (1990a).

Plant Culture, Growth Measurements, and Drought Stress Treatments

The rice cultivar used in this experiment (cv. IR-72) is grown throughout Southeast Asia. Rice was direct seeded by hand into 11 rows 0.18 m apart in each chamber on 15 July 1994. The plants were thinned to 200 plants m^{-2} , and flood water was applied on 20 July. Shades made of black, densely-woven, polypropylene fibers were maintained at canopy height along the outside of each chamber to provide a light environment similar to that found created by border rows in a field crop. On 20 July, prior to flooding, the soil in each chamber was fertilized with P and K at a rate of 9.0 g m^{-2} . Nitrogen as urea was applied at 16.5 g N m^{-2} four times during the growing season at 17, 38, 76, and 95 days after planting (DAP). The soil used was the top soil from a Kendrick fine sand (a member of the loamy, siliceous, hyperthermic, family of Arenic Paleudults).

Rice plants were destructively sampled at 19, 32, 52, 80, and 96 DAP. At 19 and 32 DAP, seven plants were sampled while at 52, 80, and 96 DAP 20 plants were sampled from each chamber. At final harvest, dry weight of each of 15 plants from each of three rows (45 plants total) from each chamber were measured as previously described. Each sampled plant was detached at ground level and dry weights were determined after oven drying at 70°C for 48 h.

Since the response of rice to drought stress depends on crop growth stage (IRRI 1982) the following water management treatments were selected: continuously flooded (CF) controls, drought imposed at panicle initiation (PI), drought imposed at anthesis (ANT) and drought imposed at both panicle initiation and anthesis (PI and ANT). This experiment was conducted with eight chambers, four maintained at each of the two CO_2 treatments. Of the four chambers in each CO_2 treatment, one was kept flooded season-long while the other three chambers experienced drought at either PI, ANT or PI and ANT. In all cases, drought treatments were imposed by shutting off the paddy water supply and unplugging the base of the lysimeter to drain the soil.

Our goal in this experiment was to impose similar levels of physiological stress rather than similar durations of stress. In order to impose similar physiological levels of drought, canopy net photosynthesis (P_n) measured at 300 s in

tervals (Baker et al., 1997a) was used as a diagnostic to determine the day for terminating the drought by reflooding the chambers. In all cases, the drought was terminated on the day when P_n became negative in high light (e.g., PAR > 1000 $\mu\text{mol photons m}^{-2}$). At this point the plants were visibly wilted and the leaves tightly rolled.

Statistical Analysis

In the 1994 drought study, where possible, prior to the ANT drought stress treatments, means and standard errors were calculated for the plant parameters measured during the destructive samplings using replicated chambers. This resulted in data points being the mean of four chambers ($n = 4$) at 19, 32, and 52 DAP and two chambers ($n = 2$) at 76 and 95 DAP. For the plant sampling data collected at final harvest, means, standard errors and analysis of variance were based on three rows ($n = 3$) containing 15 plants each for each chamber. As in previous experiments with rice at this location, within chamber estimates of variance were similar to that measured between replicated chambers. To describe trends in the data, linear and polynomial regression equations were fit via least squares linear regression.

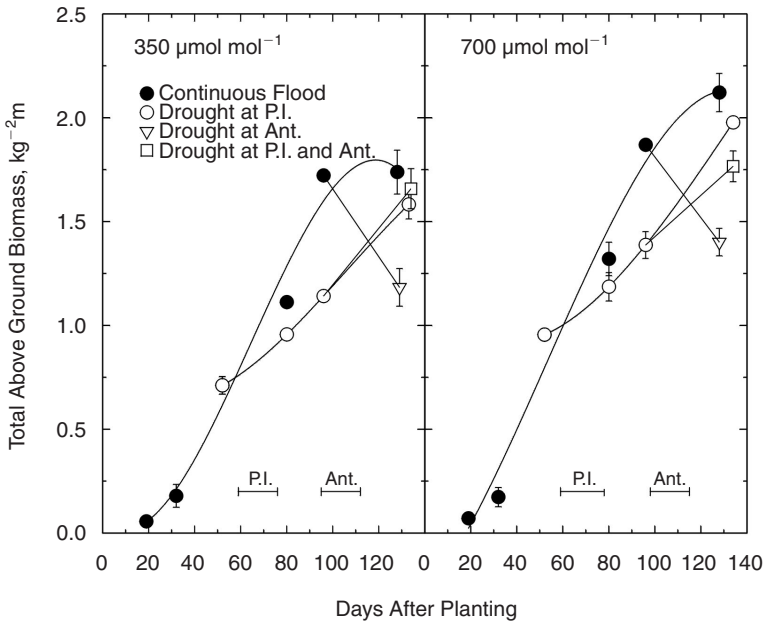
RESULTS AND DISCUSSION

Growth and Yield

Shown in Figure 1 are the seasonal trends in aboveground biomass accumulation for the CO_2 and water management treatments. In the continuously flooded controls, CO_2 enrichment resulted in a 29% increase in final aboveground biomass while drought stress reduced biomass accumulation in both CO_2 treatments. Although CO_2 enrichment generally increased biomass production, quite similar patterns in biomass accumulation were observed among the water management treatments in both CO_2 treatments.

In both CO_2 treatments, the ANT drought treatment reduced aboveground biomass far more severely than that of the PI or PI and ANT treatments (Figure 1). These differences in seasonal trends in aboveground biomass among the water management treatments were largely due to differences in leaf area and leaf biomass (Baker et al. 1997a). Visual observations of destructively sampled plants following drought stress showed that the plants responded to the drought largely by shedding lower, older leaves on the culms. This effect was especially pronounced in the ANT drought treatment. These large reductions in biomass and leaf area of the ANT compared with the PI and ANT appear to suggest that the PI drought, in some way, acclimated or hardened the plants to withstand the subsequent ANT drought.

FIGURE 1. Seasonal trends in total above ground biomass for rice grown to maturity in two atmospheric CO₂ concentrations and subjected to four water management treatments. Vertical bars are twice the standard error for each mean. Data points are means of four chambers for 19, 32, and 52 days after planting (DAP), two chambers for 76 and 95 DAP and individual chamber means at final harvest. Final harvest standard error bars were obtained from three rows containing 15 plants each. Horizontal bars labeled PI and ANT indicate average durations for the droughts imposed at panicle initiation and anthesis, respectively. (Adapted from Baker et al. 1997a.)



Final grain yield, yield components, final total above ground biomass, and harvest index are shown in Table 1. In the CF treatment, CO₂ enrichment resulted in a 28% increase in grain yield. Drought treatment tended to lower the percentage increases in grain yield due to CO₂ enrichment, especially for the PI and ANT treatment. As in previous experiments at this location with the rice cultivar IR-30 (Baker et al., 1993a), the increases in grain yield with CO₂ enrichment were associated with more panicles plant⁻¹.

In both CO₂ treatments, the effect of drought stress on final seed yield was small except for the ANT drought, which was, reduced by 44 and 53% with respect to the CF treatment, respectively (Table 1). The reductions in seed mass and the lack of significant water management treatment effects on number of

TABLE 1. Rice grain yield, components of yield, total above ground biomass and harvest index for rice (cv. IR-72) grown season-long in two atmospheric CO₂ concentrations and four water management regimes.

CO ₂	Water treatment	Grain yield	Panicle plant ⁻¹	Filled grain	Grain mass	Biomass	Harvest index
μmol mol ⁻¹		Mg ha ⁻¹	no. plant ⁻¹	no. panicle ⁻¹	mg seed ⁻¹	kg m ⁻²	kg kg ⁻¹
350	CF	6.5	4.3	37.6	19.7	1.7	0.37
	PI	6.6	4.5	36.5	20.0	1.6	0.40
	Ant.	4.5	4.1	32.2	16.3	1.2	0.38
	PI & Ant.	6.7	4.4	40.9	17.5	1.7	0.39
700	CF	8.3	4.9	38.8	20.4	2.2	0.34
	PI	8.3	4.8	44.0	20.1	2.0	0.41
	Ant.	5.4	4.5	36.6	16.1	1.4	0.37
	PI & Ant.	7.2	4.2	41.7	20.5	1.8	0.40
----- F-Values -----							
CO ₂ concentration		6.8 *	4.9 *	3.2 NS	4.2 NS	7.3 *	0.1 NS
Water treatment		7.4 **	1.7 NS	3.1 NS	19.5 **	5.9 **	4.5 *
CO ₂ * Water		0.6 NS	1.9 NS	0.7 NS	3.4 *	0.6 NS	0.8 NS

**, * Significant at the 0.01 and 0.05 probability levels, respectively. NS = Not significant.

¹ CF = Continuously flooded, PI = drought at panicle initiation, Ant. = drought at anthesis, PI + Ant. = drought at both panicle initiation and anthesis.

filled grain panicle⁻¹ (Table 1) indicates that drought in the ANT treatment reduced grain yield mainly by reducing assimilate supply to the grain during seed fill rather than affecting the flowering process. Drought stress during grain fill has also been shown to reduce grain weight in previous drought studies on rice (IRRI, 1982) presumably due to reduced assimilate supply.

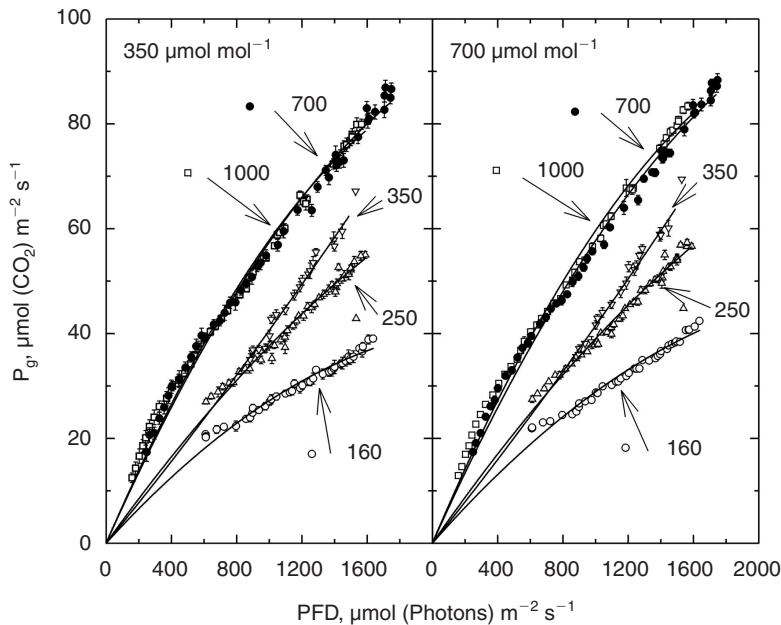
Tests for Photosynthetic Acclimation

One method to detect possible canopy-scale photosynthetic acclimation to long-term CO₂ is to grow plants for long periods (weeks or months) at two or more CO₂ and then compare their photosynthetic light responses for brief periods under a common CO₂. The hypothesis being tested here is that previous long-term CO₂ exposure treatment does not affect current short-term photosynthetic rate vs. CO₂ relationships. Additional measurements may then be made to quantify the specific acclimation response. These acclimation responses could conceivably be traced to changes in gross morphology (e.g., changes in leaf thickness or specific leaf weight) or changes in the photosynthetic biochemistry of the plant (e.g., changes in the amount and/or activity of Ruisco).

Shown in Figure 2 are comparisons of canopy P_g vs. PFD for the short-term CO_2 switching experiment conducted during the morning hours from 45 to 49 DAP. The second order polynomial regression models fit each day's data well for both long-term CO_2 treatments with uncorrected (intercept forced to zero) R^2 values exceeding 0.99 in all cases.

In order to develop a photosynthetic response curve to CO_2 at high light, the regression equations in Figure 2 were solved by setting PFD to 1600 μmol (photons) $m^{-2} s^{-1}$. These estimates of P_g are plotted against the respective short-term CO_2 switch treatment (Figure 3) for both the 350 and 700 $\mu mol mol^{-1} CO_2$ long-term treatments. A two stage-segmented model consisting of a second order polynomial for the lower, curved portion of the response and a straight line for the upper, saturated P_g section was iteratively fit simultaneously in order to describe the data. Using this model to estimate P_g for $PFD = 1600 \mu mol$ (photons) $m^{-2} s^{-1}$ at 350 and 700 $\mu mol mol^{-1}$ indicates

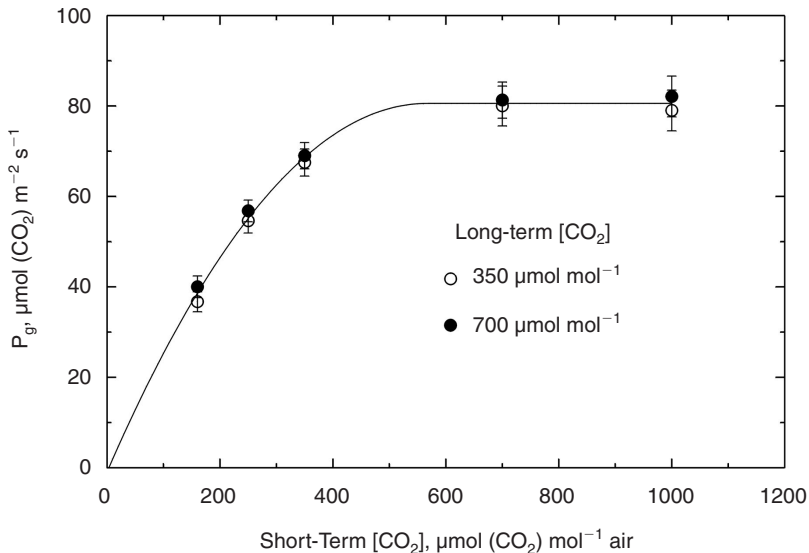
FIGURE 2. Canopy gross photosynthesis (P_g) vs. photon flux density (PFD) curves for rice grown long-term at 350 and 700 $\mu mol CO_2 mol^{-1}$ air and subjected to short-term (< 6 h) CO_2 treatments of 160, 250, 350, 700, and 1000 $\mu mol mol^{-1}$ from 45 to 49 DAP. Each data point is the mean of 4 chambers ($n = 4$) at a particular PFD level. Error bars are \pm SE of the mean. Curves are second-order polynomials fit to each day's data. (Adapted from Baker et al. 1997b.)



that doubling CO_2 across this range resulted in a 17.4% increase in P_g . These tests for canopy-scale photosynthetic acclimation of rice indicate little difference between long-term CO_2 treatments of 350 and 700 $\mu\text{mol mol}^{-1}$ for the rice cultivar IR-72.

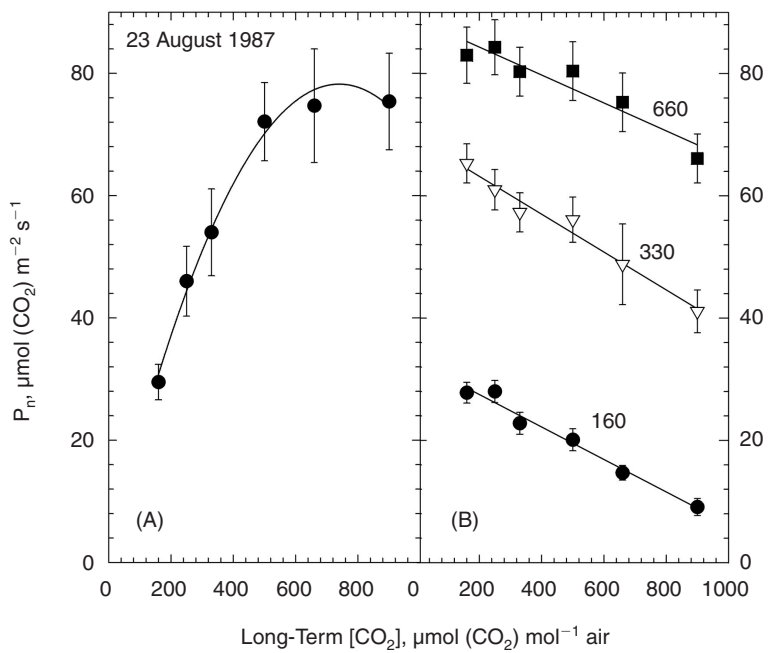
Still, in this same experiment, Vu et al. (1998) found reductions in single-leaf Rubisco content ranging between 6 to 22% for the 700 $\mu\text{mol mol}^{-1}$ compared with the 350 $\mu\text{mol mol}^{-1}$ CO_2 treatments. Thus, while photosynthetic acclimation responses in terms of enzyme down-regulation may be detected at the biochemical level, these effects may or may not result in a detectable loss of canopy-scale photosynthetic capacity when measured using gas exchange techniques. Indeed, Osborne et al. (1998) found that acclimation responses of wheat (*Triticum aestivum* L.) leaf photosynthesis to elevated CO_2 depended on both the vertical position of the leaf within the canopy and the leaf developmental stage.

FIGURE 3. Canopy gross photosynthesis (P_g) for the 350 $\mu\text{mol mol}^{-1}$ (open circle) and 700 (closed circle) long-term CO_2 treatments vs. short-term CO_2 treatments of 160, 250, 350, 700, and 1000 $\mu\text{mol mol}^{-1}$. Each data point is the solution of polynomial regression models shown in Figure 1 with PFD set to 1600 $\mu\text{mol (photons) m}^{-2} \text{s}^{-1}$. Error bars represent $\pm 95\%$ confidence limit intervals. The regression curve is a two-stage segmented model consisting of a second order polynomial (lower, curved portion) and a straight line (upper saturated portion). (Adapted from Baker et al. 1997b.)



Shown in Figure 4 are similar CO₂ cross-switches to test for photosynthetic acclimation to long-term CO₂ for the rice cultivar IR-30 in 1987 (Baker et al., 1990a). In that experiment, Baker et al. (1990a) grew rice season-long at a wide range of long-term CO₂: subambient (160 and 250 μmol mol⁻¹), ambient (330 μmol mol⁻¹) and superambient (500, 660, and 900 μmol mol⁻¹) (Figure 4a). They compared P_n light responses for all six long-term CO₂ under three common short-term CO₂: 160, 330 and 660 μmol mol⁻¹ (Figure 4b). Across this wide range of CO₂, including subambient CO₂, there was clear evidence of a down-regulation of P_n (Figure 4b). In that experiment, total plant tissue nitrogen content (Baker et al., 1992) and both Rubisco content and activity (Rowland-Bamford et al., 1991) decreased with increasing long-term CO₂ treatment.

FIGURE 4. (A). Canopy net photosynthesis (P_n) vs. long-term CO₂ acclimation treatment for rice canopies at 61 days after planting in 1987. (B). Comparison of canopy net photosynthesis (P_n) vs. long-term CO₂ acclimation treatment for short-term CO₂ of 160, 330, and 660 μmol mol⁻¹ at 62-67 days after planting. All P_n estimates are from regressions equations of P_n vs. PFD with PFD set to 1500 μmol photons m⁻² s⁻¹. Vertical bars represent 95% confidence intervals. (Adapted from Baker et al. 1990.)



Using the data in Figure 4 and extrapolated to a PFD of $1500 \mu\text{mol (photons)} \text{ m}^{-2} \text{ s}^{-1}$ there was clear evidence of a down-regulation of P_n across the long-term CO_2 from 160 to 900. For example, when measured at a common short-term CO_2 of $160 \mu\text{mol mol}^{-1}$, P_n decreased almost three fold from 27.8 to $9.1 \mu\text{mol m}^{-2} \text{ s}^{-1}$ across the long-term CO_2 from 160 to $900 \mu\text{mol mol}^{-1}$. The majority of this down-regulation response occurred across the subambient long-term CO_2 range from 160 to $330 \mu\text{mol mol}^{-1}$. When comparing only the 330 and $660 \mu\text{mol mol}^{-1}$ long-term CO_2 under the short-term CO_2 of $330 \mu\text{mol mol}^{-1}$ resulted in P_n estimates were 57.3 and $48.8 \mu\text{mol m}^{-2} \text{ s}^{-1}$, respectively. Under the short-term CO_2 of $660 \mu\text{mol mol}^{-1}$, P_n estimates were 80.3 and $75.3 \mu\text{mol m}^{-2} \text{ s}^{-1}$, respectively (Figure 4).

A nearly universal finding in CO_2 enrichment studies, including those on rice, are increases in soluble carbohydrate or total nonstructural carbohydrate (TNC) concentration of leaves and other organs for plants grown under CO_2 enrichment (Rowland-Bamford, 1996; Vu et al., 1997; 1998). The increased TNC is often attributed to enhanced photosynthesis under CO_2 enrichment and carbohydrate concentration is known to modulate the expression of many genes, including photosynthetic genes (Koch, 1996; Jang and Sheen, 1997).

Recently, Gesch et al. (1998) grew rice at ambient ($350 \mu\text{mol mol}^{-1}$) and elevated ($700 \mu\text{mol mol}^{-1}$) CO_2 . They switched these CO_2 treatments during the late vegetative stage and measured changes in mRNA for the synthesis of the small subunit of Rubisco (*rbcS*) in both growing and fully expanded leaves. They found that within 24 h, plants switched from ambient to elevated CO_2 had a 15 and 23% reduction in *rbcS* mRNA for growing and expanded leaves, respectively. For the plants switched from elevated to ambient CO_2 , *rbcS* mRNA was decreased by 27 and 11% for growing and expanded leaves, respectively. They concluded that although soluble carbohydrates may be important in the regulation of *rbcS* expression, changes in total carbohydrate pool size alone could not explain the rapid changes in gene expression that they observed.

These results for the rice cultivar 'IR-30' grown at 330 and $660 \mu\text{mol mol}^{-1}$ and those for the rice cultivar 'IR-72' grown at 350 and $700 \mu\text{mol mol}^{-1}$ suggest that across the range from current ambient CO_2 (near $360 \mu\text{mol mol}^{-1}$) to the approximate doubling of CO_2 projected for the mid- to late 21st century, canopy-scale photosynthetic acclimation of these rice cultivars to CO_2 may not be a large factor governing rice photosynthesis responses to CO_2 . Quantitative differences in these tests for photosynthetic acclimation (e.g., between Figures 2 and 4) may be due to the two different rice cultivars used, differences in crop growth stages when the tests were made and/or the CO_2 ranges used in the two experiments.

The results in Figure 3 also point to a complete CO_2 saturation of P_g near $500 \mu\text{mol mol}^{-1}$ for the rice cultivar 'IR-72' and support previous findings for

the rice cultivar 'IR-30' (Figure 4a). For 'IR-30' Baker et al. (1990a, b, c; 1992) found that phenological development, growth, tillering, final seed yield, P_n , canopy light utilization efficiency, and canopy dark respiration rates all increased with CO_2 from 160 to 500 $\mu\text{mol mol}^{-1}$ with little change from 500 to 900 $\mu\text{mol mol}^{-1}$. This very flat leveling off of rice responses to elevated CO_2 contrasts with that of other C_3 crop species such as soybean (Campbell, 1990; Baker et al., 1993a). Due to this leveling off of responses above 500 $\mu\text{mol mol}^{-1}$, Baker et al. (1990a) suggested selecting or screening rice cultivars for increased response to CO_2 enrichment in order to more fully take advantage of future increases in global atmospheric CO_2 since the photosynthesis and grain yield responses to CO_2 enrichment may not be the same for all rice cultivars. Indeed, Ziska et al. (1996) reported large differences in growth and yield responses of 17 rice cultivars to both temperature and CO_2 .

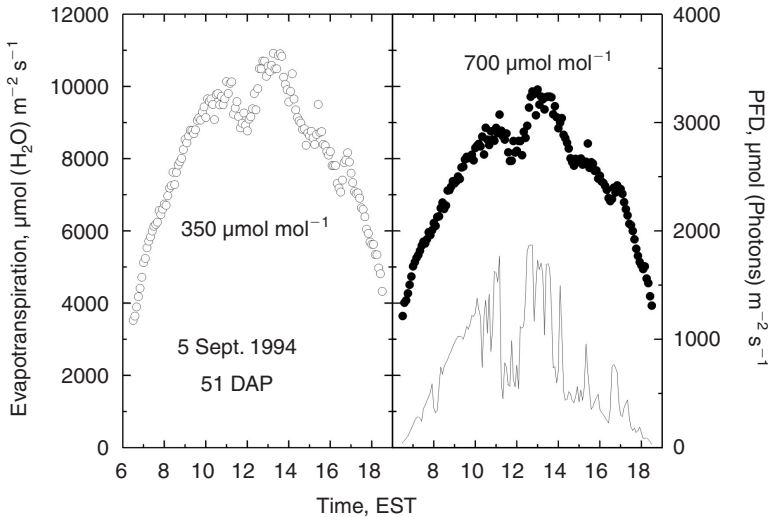
Drought and CO_2 Effects on Canopy Photosynthesis and Evapotranspiration

Carbon dioxide enrichment causes partial stomatal closure, increased stomatal resistance, and can result in reduced canopy or single leaf transpiration (Rogers et al., 1984; Jones et al., 1985; Valle et al., 1985). However, this water savings from CO_2 enrichment is greater on a per unit leaf area basis rather than a total canopy basis. Part of the reason for this difference is that leaf area is also increased so that the surface area available for transpiration increases. This increase in canopy leaf area acts to offset some of the water savings from CO_2 enrichment (Jones et al., 1985; Allen et al., 1985). Furthermore, the stomatal closure caused by CO_2 enrichment results in increased leaf temperature, and thus an increase in the vapor pressure gradient between leaf and air.

Shown in Figure 5 is an example of CO_2 treatment effects on rice canopy evapotranspiration. In this experiment, the water loss represents evaporation from the paddy as well as canopy transpirational water loss. The diurnal trends in ET tracked PFD for both CO_2 treatments, with peak levels of ET for the 350 $\mu\text{mol mol}^{-1}$ CO_2 treatment being greater than that of the 700 $\mu\text{mol mol}^{-1}$ treatment. Comparisons of daily totals of P_n , ET and WUE for this same day (52 DAP) showed that CO_2 enrichment from 350 to 700 $\mu\text{mol mol}^{-1}$ resulted in a significant 20.5% increase in total daily P_n and 10.2% reduction in total ET (Baker et al., 1997b). In general, similar reductions in ET due to CO_2 enrichment, typically ranging from 9 to 11%, were observed throughout most of the growing season prior to the beginning of canopy leaf senescence. These trends in total daily P_n and ET resulted in significantly greater estimates of WUE with CO_2 enrichment (Baker et al., 1997b).

Shown in Figure 6 are diurnal trends in canopy P_n measured near the end of the PI drought at 75 DAP. Throughout most of the day, P_n was higher in the

FIGURE 5. Diurnal trends in photosynthetic photon flux density (PFD, solid line) and evapotranspiration rates for the 350 (open symbols) and 700 (closed symbol) $\mu\text{mol mol}^{-1}$ CO_2 treatments at 52 days after planting, prior to the PI drought stress treatment. Each data point is the mean of 4 chambers ($n = 4$). (Adapted from Baker et al. 1997b.)

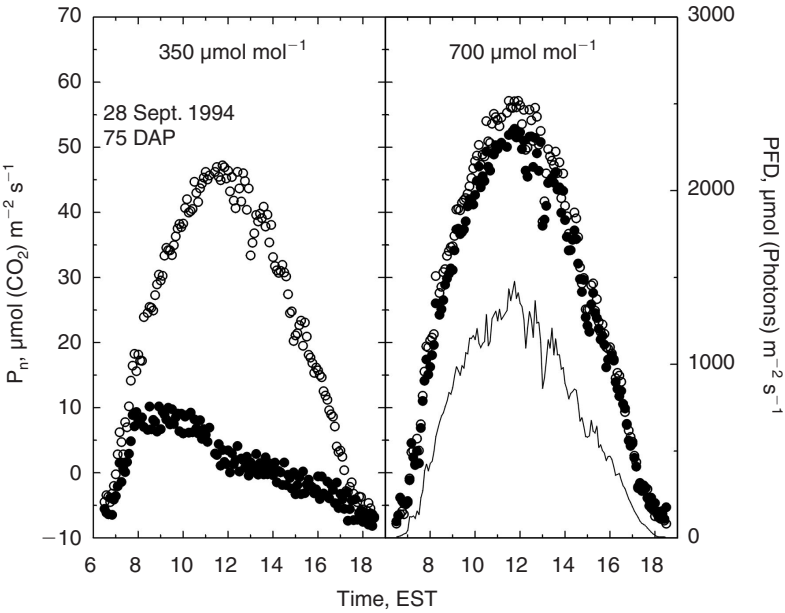


700 than the 350 $\mu\text{mol mol}^{-1}$ CO_2 treatments, for both the CF controls and PI drought treatments. Also, canopy P_n of the PI drought stress treatments were much lower than the flooded controls in the 350 than the 700 $\mu\text{mol mol}^{-1}$ CO_2 treatment (Figure 6). The 350 $\mu\text{mol mol}^{-1}$ PI drought stress treatments were reflooded and drought stress terminated the following day (76 DAP) while the 700 $\mu\text{mol mol}^{-1}$ PI drought stress treatments required an extra 1 to 2 days to exhaust the soil water supply (Baker et al., 1997a) and reduce P_n to similar levels as those shown for the 350 $\mu\text{mol mol}^{-1}$ PI drought treatments. The time courses of soil water potential measurements for the PI drought stress treatments given by Baker et al. (1997a) also indicate that the 700 $\mu\text{mol mol}^{-1}$ treatment lagged that of the 350 $\mu\text{mol mol}^{-1}$ by one to two days in soil water depletion.

Drought and CO_2 Effects on Apparent Canopy Dark Respiration

In discussing CO_2 treatment effects on R_d , a functional distinction is often made between 'direct' and 'indirect' effects of CO_2 on R_d . A short-term or immediate effect of CO_2 on R_d is referred to as a 'direct effect.' An 'indirect' ef-

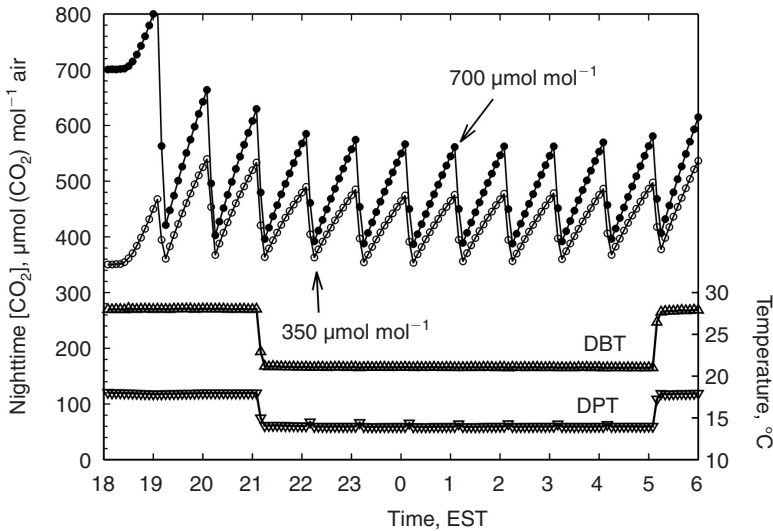
FIGURE 6. Diurnal trends in photosynthetic photon flux density (PFD, solid line) and canopy net photosynthetic rates (P_n) for the 350 and 700 $\mu\text{mol mol}^{-1}$ CO_2 treatments at 75 DAP, near the end of the PI drought stress treatment. Open and closed symbols are for the continuously flooded control and PI drought stress treatments, respectively. (Adapted from Baker et al. 1997b.)



fect of CO_2 on R_d results from growing plants for long periods of time at elevated CO_2 . These indirect effects typically manifest themselves in terms of changes in plant biomass, nonstructural carbohydrate concentration, tissue nitrogen concentration or protein content and often result in changes in growth and/or maintenance components of respiration (Amthor, 1991; Baker et al., 1992; Griffin et al., 1993; Amthor, 1997). Work by Bunce and Ziska (1996) and Ziska and Bunce (1998) points to the need for experimental procedures that can distinguish between long-term indirect effects vs. the persistence of a short-term direct effect. To detect a direct effect it is necessary to conduct short-term switching of CO_2 treatments (e.g., ambient treatment measured for a short time at ambient and then elevated CO_2 and elevated treatment measure for a short time at ambient and then elevated CO_2 , Ziska and Bunce, 1994).

An example of nighttime chamber CO_2 during the venting procedure used to measure R_d is shown in Figure 7. These estimates of R_d were corrected for chamber leakage rate using the nitrous oxide leak detection system described

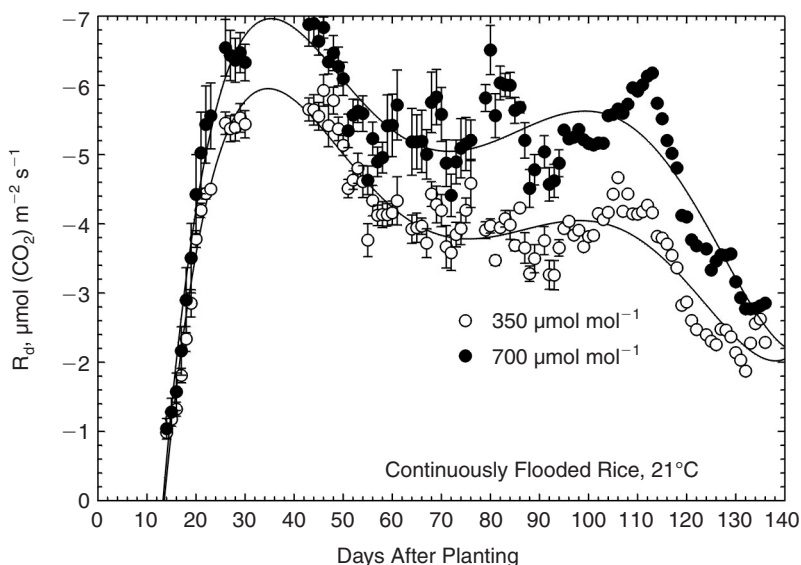
FIGURE 7. Example of chamber environmental controls for nighttime dew point air temperature (DPT), dry bulb air temperature (DBT), and CO_2 used to calculated canopy apparent respiration (R_d) on 5 Sept. 1994, 52 days after planting. Open and closed circles indicate rice canopies exposed to 350 and 700 $\mu\text{mol mol}^{-1}$ CO_2 treatments during the day light hours, respectively. (Adapted from Baker et al., 2000a.)



by Baker et al. (2000a). Also, R_d calculated in this way may also include some root respiration since CO_2 exchange through the rice plant aerenchyma system probably occurs as freely as oxygen exchange and CH_4 effluxes (Nouchi et al., 1990; Allen, 1997).

In general, the drought stress treatments reduced R_d due to accelerated leaf senescence and a reduction in above ground biomass (Baker et al., 2000b). Shown in Figure 8 are seasonal trends in R_d at a nighttime dry bulb air temperature of 21°C for both daytime CO_2 treatments in the continuously flooded (CF) control treatments. Maximum seasonal values of R_d occurred at around 30 to 40 DAP for both CO_2 treatments (Figure 8). This time period (30-40 DAP) also coincides with complete canopy closure and seasonal maximum rates of canopy photosynthesis (Baker et al., 1997a,b). For most of the growing season, R_d of the 700 $\mu\text{mol mol}^{-1}$ treatment exceeded that of the 350 $\mu\text{mol mol}^{-1}$ treatment CO_2 by about 1 to 2 $\mu\text{mol m}^{-2} \text{s}^{-1}$. These measurements were made shortly after the vent gates were closed (Figure 7) at a similar and near ambient chamber CO_2 . Therefore, these differences in R_d are largely due

FIGURE 8. Seasonal trends in canopy apparent respiration (R_d) for rice exposed to 350 and 700 $\mu\text{mol mol}^{-1}$ CO_2 treatments during the day light hours. Vertical bars are \pm S.E. (Adapted from Baker et al. 2000b.)



to the secondary effects of CO_2 on plant biomass and plant tissue composition and are thus considered 'indirect effects' (Baker et al., 1992; 2000a, b).

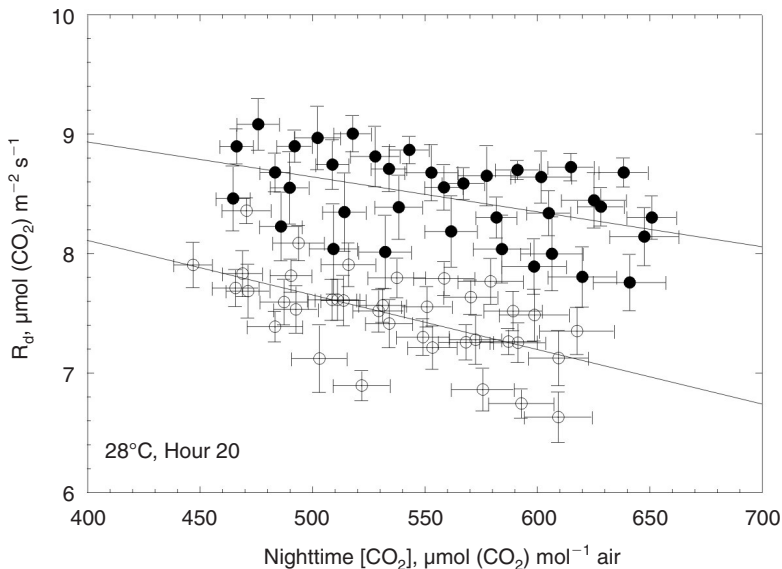
Baker et al. (2000a) tested for 'direct effects' of elevated CO_2 on R_d by utilizing the range of CO_2 produced during the venting procedures (Figure 7). Direct inhibition of respiration by elevated CO_2 is not a universally observed phenomenon (Gifford, 1995; Amthor, 2000; Jahnke, 2001; Bruhn et al., 2002; and reviews by Wullschlegel et al., 1994 and Amthor, 1997) and can apparently be altered by air temperature treatment (Ziska and Bunce, 1993) or long-term CO_2 growth concentration (Thomas and Griffin, 1994; Bunce and Ziska, 1996). For example, when whole soybean plants were switched from low to high CO_2 , leaf respiration was always reduced but this reduction was 50% less for plants grown in elevated CO_2 compared with near ambient CO_2 (Thomas and Griffin, 1994).

Baker et al. (2000a) measured whole canopy dark respiration (R_d) with rising chamber CO_2 across short-term air temperature switches ranging from 21 to 40°C. They found a rapid and reversible, direct inhibition of canopy dark respiration R_d with rising chamber CO_2 for air temperatures above 21°C. The direct inhibition of R_d by rising chamber CO_2 at air temperatures above 21°C

was larger for the 350 compared with the 700 $\mu\text{mol mol}^{-1}$ daytime CO_2 treatment. For example, shown in Figure 9, at 28°C, and across an extrapolated CO_2 range from 350 to 700 $\mu\text{mol mol}^{-1}$ the decline in R_d amounted to a 19 and 11% inhibition of R_d for the 350 and 700 $\mu\text{mol mol}^{-1}$ daytime CO_2 treatments, respectively.

Several mechanisms for this direct effect have been proposed, including dark CO_2 fixation and direct inhibition or deactivation of one or more respiratory enzymes (Amthor, 1991). Work by Gonzalez-Meler et al. (1996) and review by Drake et al. (1999) indicate that direct inhibition of cytochrome *c* oxidase and succinate dehydrogenase by elevated CO_2 may at least be a part of the basis for this response. On the other hand, systematic errors or artifacts in measuring respiration have also been proposed to explain reports of a direct inhibition of R_d with increased CO_2 . Two possible artifacts are a dilution of the air surrounding the leaf by transpired water or an unaccounted for leak between the leaf cuvette and the surrounding air (Drake et al., 1999; Jahnke,

FIGURE 9. Canopy apparent respiration (R_d) vs. nighttime CO_2 at a dry bulb air temperature of 28°C for rice canopies maintained during the day at 350 (open circles) and 700 (filled circles) $\mu\text{mol mol}^{-1}$ daytime CO_2 treatments. Each data point is the mean of four replicate chambers averaged at the same point in time. Vertical and horizontal bars are \pm SE of the mean. Data are from 46 to 50 days after planting in 1994. (Adapted from Baker et al. 2000a.)



2001; Bruhn et al., 2002). In this experiment (Baker et al., 2000a and Figure 9), moisture was removed from the gas sample by running the sample lines through a refrigerated water trap (4°C) that was automatically drained twice a day while chamber leakage rates were corrected for using a nitrous oxide leak detection system.

CONCLUSIONS

We conclude that in the absence of air temperature increases, future global increases in CO₂ should promote rice growth and yield while providing a modest reduction of near 10% in water use and so increase drought avoidance. Photosynthetic rate saturated with respect to CO₂ near 500 μmol mol⁻¹. Carbon dioxide enrichment significantly increased both canopy net photosynthetic rate (21 to 27%) and water-use efficiency while reducing evapotranspiration by about 10%. This water saving under CO₂ enrichment allowed photosynthesis to continue for about one to two days longer during drought in the enriched compared with the ambient CO₂ control treatments.

Reductions in rice respiration following drought and re-watering appeared to be related to reductions in above-ground biomass due to accelerated leaf senescence. When compared at common, near ambient CO₂, daytime CO₂ enrichment resulted in higher R_d compared with the ambient grown controls. We also detected a rapid and reversible, direct inhibition of R_d with rising chamber CO₂ at an air temperature of 28°C.

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